THE POLLEN GRAIN MORPHOLOGY OF COLLOMIA AS A TAXONOMIC TOOL

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There is a rich variety of pollen grain forms within the family Polemoniaceae, and a species is commonly recognizable by the pollen grain characters. Furthermore, these grains are abundant—each plant producing many more grains than leaves or fruits—and the grains are more readily preservable as fossils because of their small size and resistance to deterioration. Hence a well illustrated and comparative account of the modern pollen morphology may lead to the recognition of fossil members of the Polemoniaceae.

There have been only three reports of fossil remains of the family Polemoniaceae, a Pleistocene fruit of a *Phlox* (Chaney and Mason, 1936), a Pleistocene *Polemonium* pollen grain (Godwin, 1956), and a subfossil pollen grain of *Collomia* (Hafsten, 1960). The lack of paleontological evidence renders suspect the validity of the conclusions that have been made concerning the evolution of this family (Wherry, 1944; Grant, 1959). It is questionable whether megafossils will ever yield much information about the evolutionary trends within this family, since preservation of recognizable fossil remains of these herbaceous plants or of their fruits or flowers is unlikely except under unusual circumstances. If a more abundant and more readily preserved part of the plant, such as the pollen, could be found to characteristic of a species or genus, paleobotanists and palynologists would be aided in recognizing fossil occurrences of the Polemoniaceae.

When used in conjunction with other features of a plant, pollen characteristics should aid in its taxonomic classification. According to Grant (1959, p. 35), "The Polemoniaceae is a taxonomically complex family in which generic and specific divisions have frequently been the subject of confusion and dispute." As will be evident from this study of the genus *Collomia* Nutt., pollen morphology may be as useful a taxonomic tool for the neontologist as it is for the paleontologist.

Yet almost as sparse as the information of the fossil record of the Polemoniaceae, is that concerning pollen morphology of the included genera. To date only four significant references have been made to the pollen of the genus *Collomia*. Erdtman (1952) briefly described and figured that of one form, *C. grandiflora* f. *axillaris* (Nels.) Wherry. Hafsten (1960) figured a subfossil pollen grain and identified it as the form illustrated by Erdtman. In 1959 Grant made a general survey of the pollen grain types within the family, but gave neither specific descriptions nor comparisons.

The most comprehensive study of the pollen of the Polemoniaceae has been presented by Marticorena (1961), who was concerned only with the Chilean species, and treated both of the known South American species

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in *Collomia*. Thus, to date, the pollen has been studied only of *C. grandiflora f. axillaris* and the two Chilean species out of the total of 14 species in *Collomia*. No comparative studies of the pollen of all the species of this genus have yet been published.

Material and Methods

Pollen was obtained from University of California herbarium specimens and was acetolyzed according to the micromethod of Punt (1962). The collectors and collection numbers and herbarium numbers of the specimens are given in the graph of equatorial diameters (fig. 1). Data for Fig. 1 were obtained by measuring 50 fully expanded pollen grains from each herbarium sheet. Grains whose orientation on the prepared slide allowed a polar diameter measurement were scarce, therefore fewer polar than equatorial diameter measurements were obtained. The terminology used in the description of species follows that of Erdtman (1952).

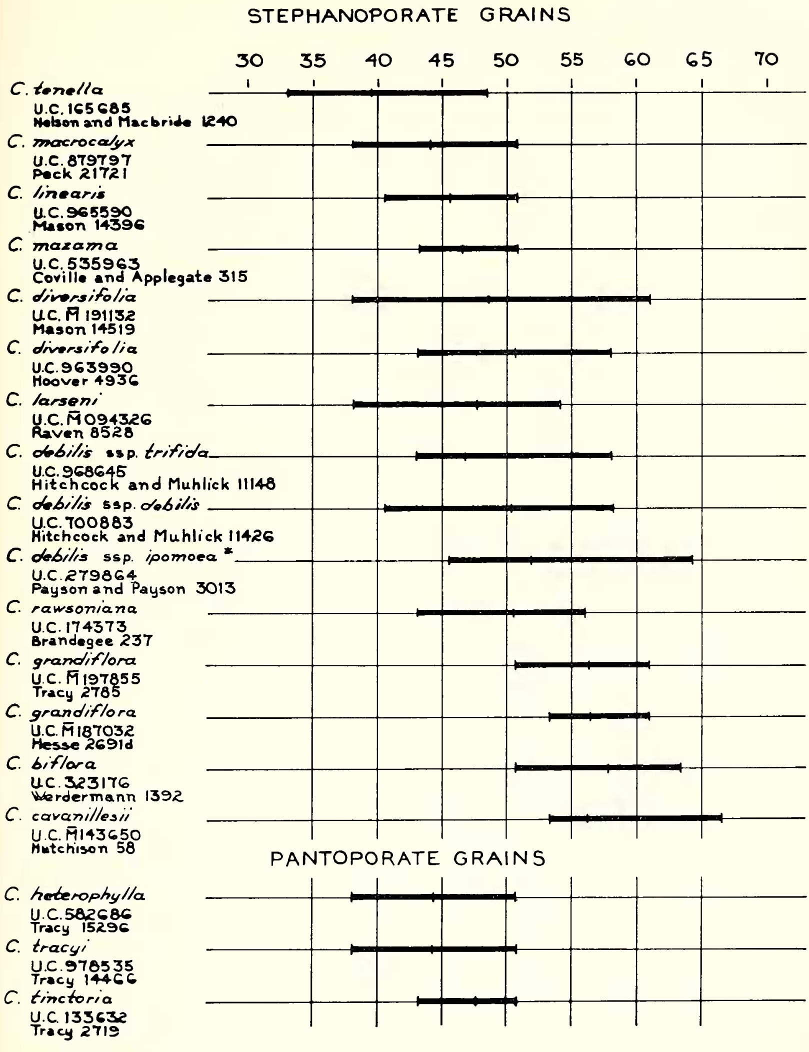
Descriptions of the Pollen Grains in Species of Collomia

C. biflora (Ruiz et Pav.) Brand. Average equatorial diameter: 57.9 μ, range: 50.8 to 63.5 μ; average polar diameter: 44.5 μ; average ratio of equatorial to polar diameter: 1.30:1 (subspheroidal, suboblate). Stephanoporate, (7)–8–(9) apertures, composite, ovate, length in nexine 7.7 μ, width 3.3 μ. Exine 2.9 μ in thickness, sexine only slightly thicker than nexine, the nexine swelling at the apertural margins; surface of sexine with subparallel and irregular ridges locally breaking up into reticulations. Figs. 20, 21.

C. cavanillesii Hook. & Arn. Average equatorial diameter: 56.2 μ, range: 53.3 to 66.7 μ; average polar diameter: 48.2 μ; average ratio of equatorial to polor diameter :1.17:1 (subspheroidal, suboblate). Stephanoporate, (6)–(7)–8–(9) apertures, composite, ovate, length in nexine 7.7 μ, width 5.5 μ. Exine 3.5 μ in thickness, sexine 1.5 times as thick as nexine, nexine swelling at apertural margins. Sexine pattern composed of continuous meandriform ridges. Figs. 22, 23.

C. debilis (S. Wats.) Greene ssp. *debilis*. Average equatorial diameter: 50.3 μ, range: 40.6 to 58.2 μ; average polar diameter: 41 μ; average ratio of equatorial to polar diameter: 1.23:1 (subspheroidal, suboblate). Stephanoporate, (6)–7–(8)–(9) apertures, composite, ovate. Aperture measurements (for species of *C. debilis* sensu lato): length in nexine 7.7–8.8 μ, width 4.4–5.5 μ. Exine 3.3 μ in thickness, sexine 1.5 times as thick as nexine, nexine swelling at apertural borders. Sexine pattern consists of subparallel ridges, whose orientation resembles the pattern of lines of force in a magnetic field whose poles are in the position of the apertures. Figs. 30. 31.

C. debilis ssp. *ipomoea* (Pays.) Wherry. Average equatorial diameter: 51.9 μ, range: 45.6 to 64.3 μ; average polar diameter: 42.7 μ; average ratio of equatorial to polar diameter: 1.22:1 (subspheroidal, suboblate). Stephanoporate, (7)–8–(9) apertures, composite, ovate. Exine 3.3 μ in thickness, sexine 1.5 times as thick as nexine, nexine swelling at the aper-



* Only 25 measurements were made.

FIG. 1. Graph showing equatorial pollen diameters of the various species of *Collomia*.

tural margins. Sexine pattern in equatorial view of grain consists of subparallel radiating ridges whose orientation resembles the pattern of lines of force in a magnetic field having the poles at the ends of the apertures. Figs. 26, 27.

C. debilis ssp. *trifida* (Pays.) Wherry. Average equatorial diameter: 47.9 μ, range: 43 to 58 μ; average polar diameter: 40 μ; average ratio of equatorial to polar diameter: 1.20:1 (subspheroidal suboblate). Stephanoporate, (7)–8–(9) apertures, composite, ovate. Exine 3 μ thick; sexine only slightly thicker than nexine, nexine swelling at the apertural borders. Sexine pattern composed of ridges subparallel in an orientation resembling the pattern of lines of force in a magnetic field having poles at the ends of the apertures. Figs. 28, 29.

C. diversifolia Greene. Average equatorial diameter: 49.6 μ, range: 38 to 61 μ; average polar diameter: 43 μ; average ratio of equatorial to polar diameter: 1.16:1 (subspheroidal, suboblate). Stephanoporate, (5)–6–(7) apertures, composite, ovate, length in nexine 6.6 μ, width 4.4 μ. Exine 3.3 μ thick, sexine 1.5 times as thick as the nexine, nexine swelling at apertural margins. Sexine pattern composed of slightly continuous subparallel ridges in a swirling design. Fig. 11.

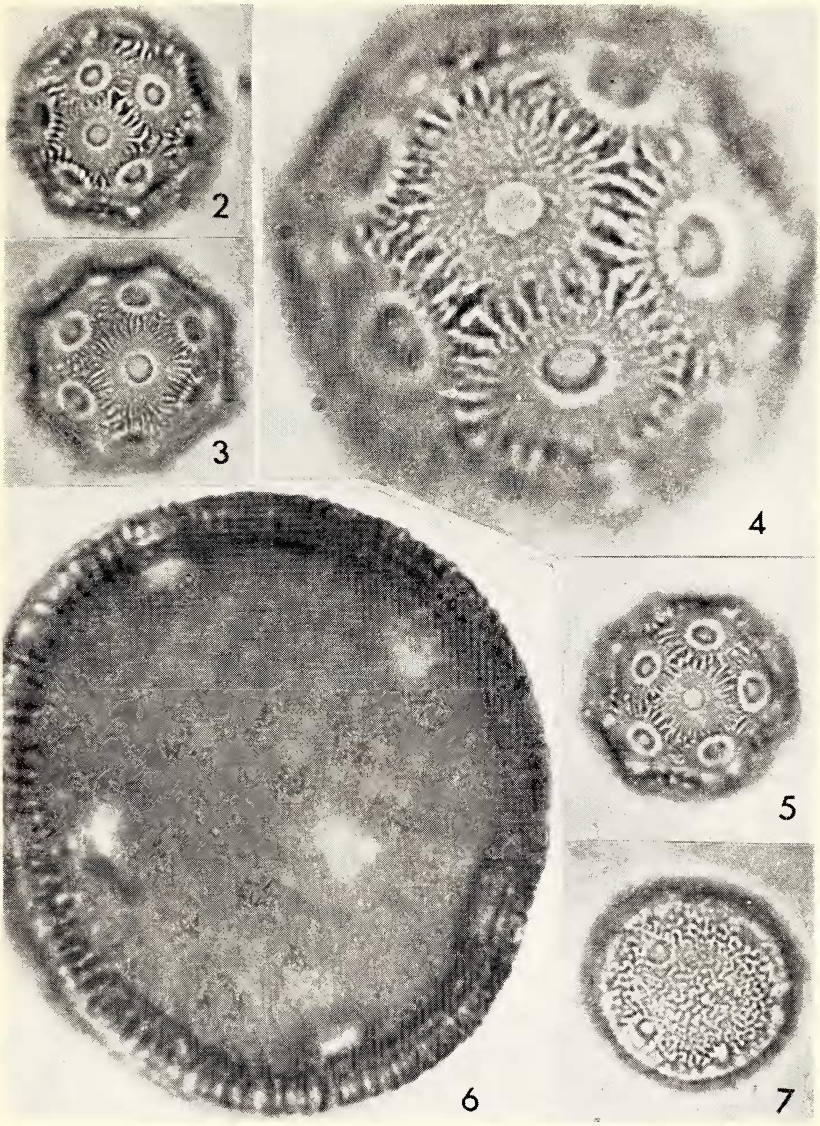
C. grandiflora Dougl. ex Lindl. Average equatorial diameter: 56.4 μ, range: 50.7 to 61 μ; average polar diameter: 43.6 μ; average ratio of equatorial to polar diameter: 1.29:1 (subspheroidal, suboblate). Stephanoporate, (7)–8–(9) apertures, composite, ovate, length in nexine 11 μ, width 4.4 μ. Exine 3.3 μ thick, sexine 1.5 times as thick as the nexine, nexine swelling at apertural margins. Sexine pattern composed of beaded ridges radiating from the poles and continuing as parallel ridges along the aperture margins. Figs. 8, 9.

C. heterophylla Hook. Average diameter: 44.3 μ, range: 38 to 50.7 μ (spheroidal). Pantoporate, 10–16 apertures, simple, circular, diameter in nexine 3 μ. Exine 3.3 μ in diameter, sexine 1.5 times as thick as the nexine, nexine swelling at apertural margins (fig. 32). Sexine ornamentation composed of sharply curved ridges tending to a somewhat reticulate pattern. Figs. 6, 7.

C. larsenii (Gray) Pays. Average equatorial diameter: 47.7 μ, range: 38 to 54 μ; average polar diameter: 40.3 μ; average ratio of equatorial to polar diameter: 1.18:1 (subspheroidal, suboblate). Stephanoporate, (6)–7–8 apertures, composite, ovate, length in nexine 8 μ, width 4.4 μ. Exine 2.6 μ thick, sexine only slightly thicker than nexine, nexine swelling at apertural margins. Sexine pattern composed of subradiating ridges passing parallel to one another around the apertures. Fig. 10.

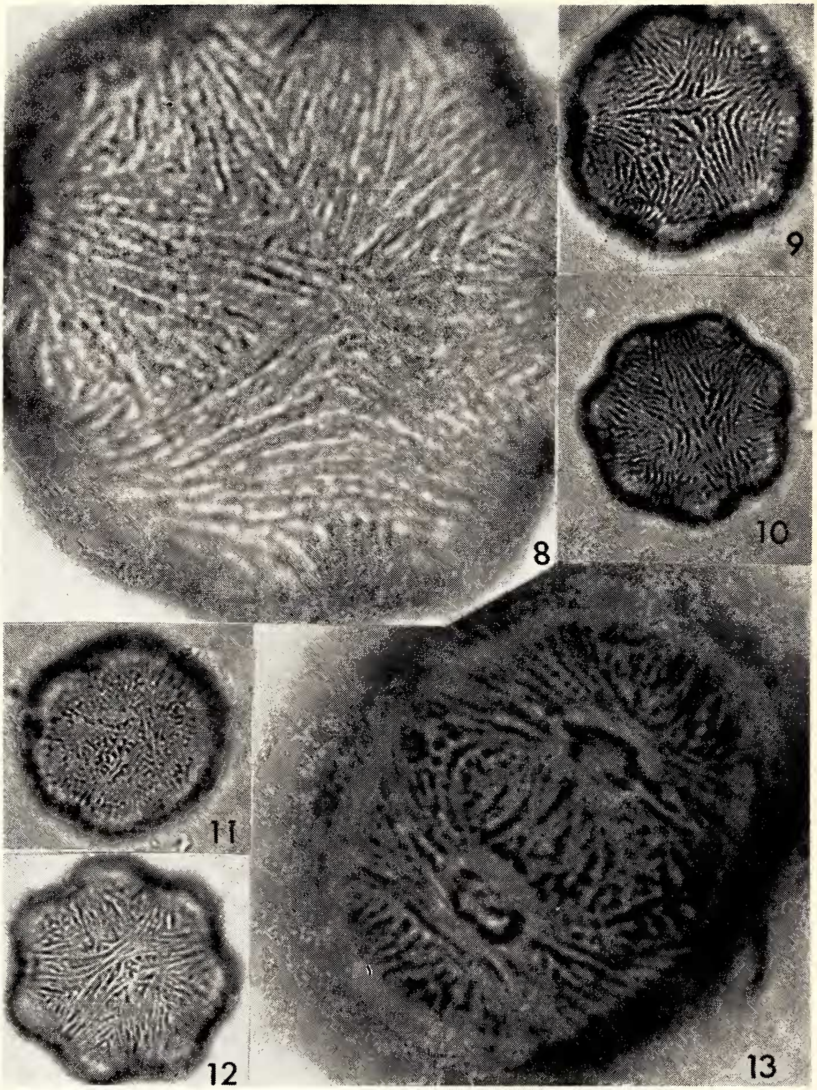
C. linearis Nutt. Average equatorial diameter: 45.6 μ, range: 40.5 to 50.8 μ; average polar diameter: 40.3 μ; average ratio of equatorial to polar diameter: 1.31:1 (subspheroidal, oblate spheroidal). Stephanoporate, 7–8–(9)–(10) apertures, composite, ovate, length in nexine 7.7 μ, width 3.3 μ. Exine 3.6 μ thick, sexine twice as thick as the nexine, nexine swelling at apertural margins (fig. 33). Sexine ornamentation composed of sharply curved ridges tending to a somewhat reticulate pattern. Figs. 14, 15.

C. macrocalyx Leib. ex Brand. Average equatorial diameter: 44.1 μ, range: 38 to 50.8 μ; average polar diameter 35.2 μ; average ratio of equatorial to polar diameter: 1.25:1 (subspheroidal, suboblate). Stephano-



FIGS. 2–7. Pollen grains of *C. tinctoria, tracyi,* and *heterophylla*; 2, 3, sexine pattern and arrangement of apertures of *C. tinctoria,* both × 640; 4, 5, sexine pattern and distribution of apertures of *C. tracyi,* × 1600 and 640, respectively; 6, optical section of *C. heterophylla,* apertures appear as light areas in center and one is shown in side view at the lower right periphery, × 1600; 7, surface view of *C. heterophylla* showing sexine ornamentation and scattered apertures, × 640.

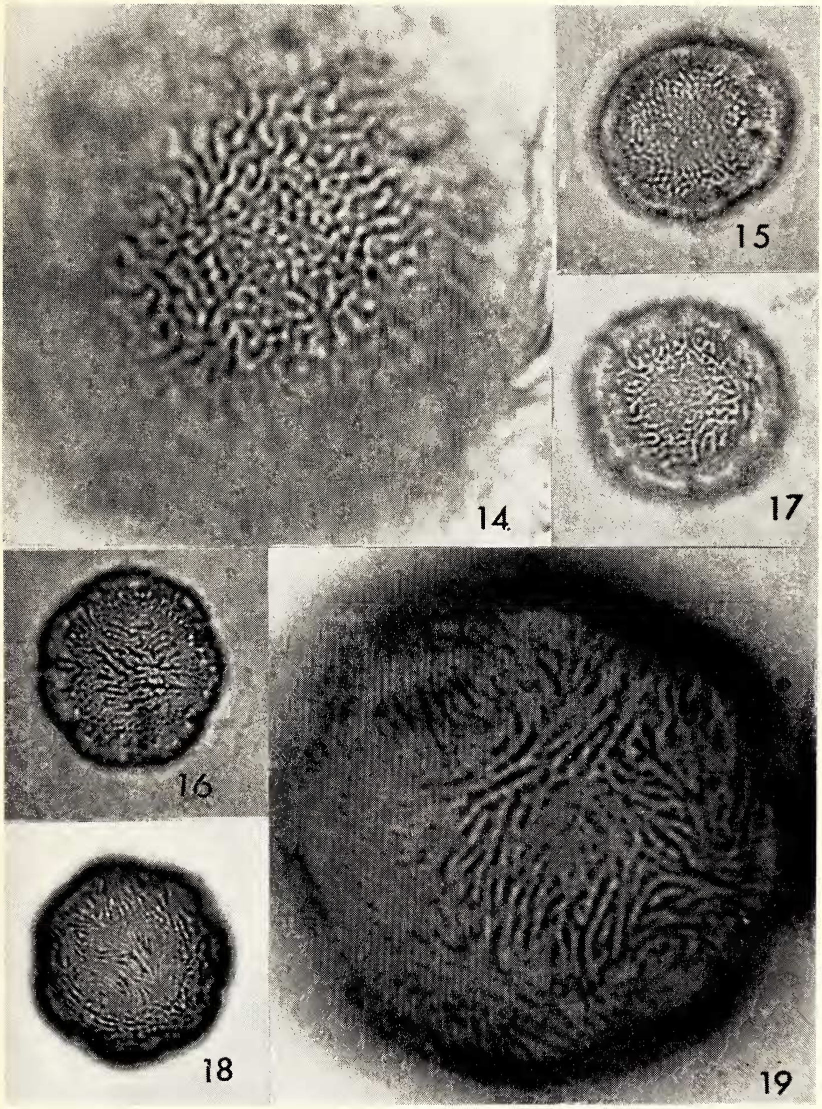
porate, (7)–8–(9) apertures, composite, ovate, length in nexine 5.5 μ, width 2.2 μ. Exine 3 μ thick, sexine 1.5 times thicker than nexine, nexine



FIGS. 8–13. Pollen grains of *C. grandiflora, larsenii, diversifolia,* and *rawsoniana*; 8, 9, polar views showing sexine ornamentation of *C. grandiflora,* × 1600 and 640 respectively; 10, polar view showing sexine ornamentation of *C. larsenii,* × 640; 11, polar view showing sexine ornamentation of *C. diversifolia,* × 640; 12, polar view showing sexine pattern of *C. rawsoniana,* × 640; 13, equatorial view of *C. rawsoniana* showing pattern of the sexine around two apertures, × 1600.

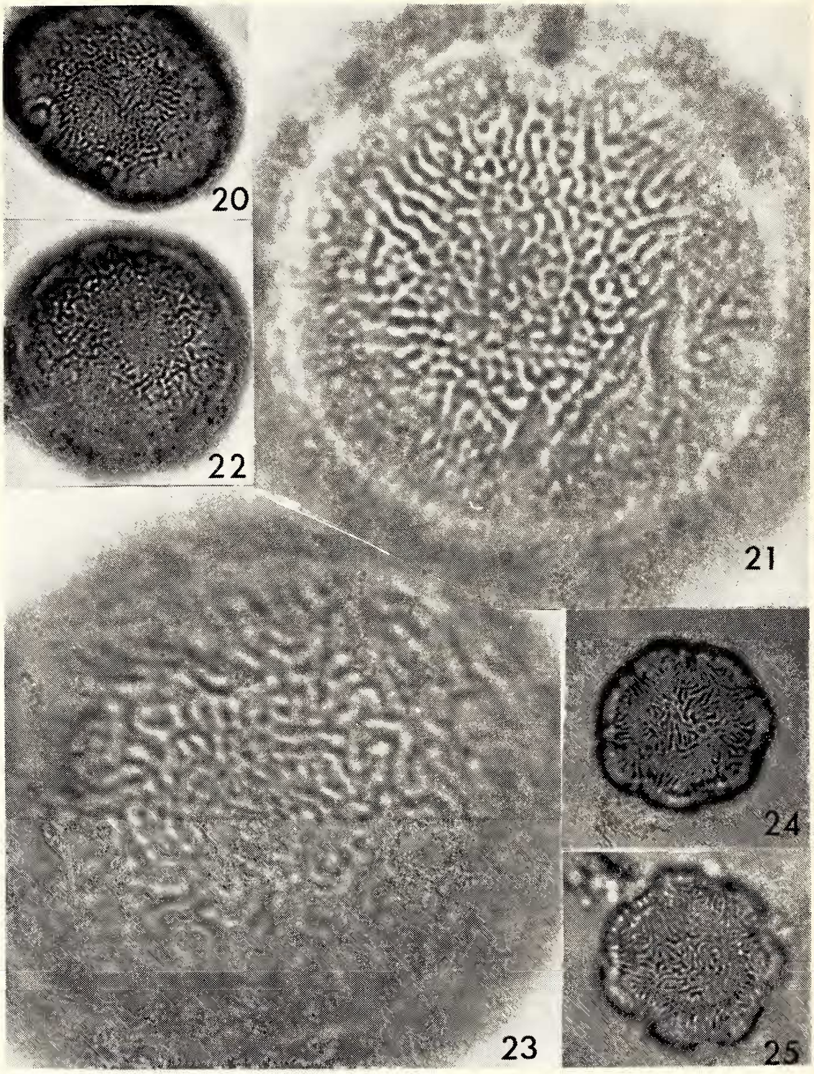
swelling at apertural margins. Sexine pattern composed of rather continuous subparallel ridges in a swirling design. Figs. 16, 17.

C. mazama Cov. Average equatorial diameter: 46.6 μ, range: 43.2 to



FIGS. 14–19. Pollen grains of *C. linearis, macrocalyx,* and *mazama*; 14, 15, polar views showing sexine pattern of *C. linearis,* × 1600 and 640 respectively; 16, 17, polar views showing sexine pattern of *C. macrocalyx,* both × 640; 18, 19, polar views showing sexine pattern of *C. mazama,* × 640 and 1600 respectively.

50.8 μ; average polar diameter: 38 μ; average ratio of equatorial to polar diameter: 1.23:1 (subspheroidal, suboblate). Stephanoporate (7)–8–(9) apertures, composite, ovate, length in nexine 5.5 μ width 3.3 μ. Exine 2.6 μ thick, sexine as thick as the nexine, nexine swelling at apertural



FIGS. 20–25. Pollen grains of *C. biflora, cavanillesii,* and *tenella*; 20, slightly tilted polar view showing sexine pattern of *C. biflora,* × 640; 21, polar view showing sexine pattern of *C. biflora,* × 1600; 22, 23, polar views showing sexine pattern of *C. cavanillesii,* × 640 and 1600 respectively; 24, 25, polar views showing sexine ornamentation of *C. tenella,* both × 640.

margins. Sexine pattern composed of rather subparallel, continuous ridges in a swirling design. Figs. 18, 19.

C. rawsoniana Greene. Average equatorial diameter: 50.5 μ, range: 43 to 56 μ; average polar diameter: 41.2 μ; average ratio of equatorial to polar diameter: 1.23:1 (subspheroidal, suboblate). Stephanoporate, 7–8–

(9) apertures, composite, ovate, length in nexine 8.8 μ, width 3.0 μ. Exine 3.6 μ thick, sexine 1.5 times as thick as the nexine, nexine swelling at apertural margins (fig. 34). Sexine pattern composed of subparallel ridges in an orientation resembling the pattern of lines of force in a magnetic field having poles at the ends of the apertures. Figs. 12, 13.

C. tenella Gray. Average equatorial diameter: 39.5 μ, range: 33 to 47.4 μ; average polar diameter: 32 μ; average ratio of equatorial to polar diameter; 1.23:1 (subspheroidal, suboblate). Stephanoporate, (6)–7–(8) apertures, composite, ovate, length in nexine 5.5 μ, width 2.2 μ. Exine 2.6 μ thick, sexine twice as thick as nexine, nexine swelling at the apertural margins. Sexine pattern composed of rather continuous subparallel ridges in swirling design of meandriform, curving ridges. Figs. 24, 25.

C. tinctoria Kell. Average diameter: 47.7 μ, range: 43.2 to 50.8 μ (spheroidal). Pantoporate, 19 to 24 apertures, simple, circular, diameter in nexine 3.9 μ. Exine 3.3 μ thick, nexine thinnest in area between pores where sexine is thickest (fig. 35). The nexine swells to 1.3 μ at the apertural margins. Each aperture is at the center of a small, deeply sunken pentagonal or hexagonal area, bordered by a broad radially grooved ridge, the slightly irregular radial grooves also extending across the polygonal area but less prominent there than on the marginal ridges. Figs. 2, 3.

C. tracyi Mason. Average diameter: 44.2 μ, range: 38 to 50.8 μ (spheroidal). Pantoporate, apertures 17 to 28, simple, circular, diameter in nexine 3.9 μ. Exine, 3.3 μ thick, the nexine thinnest in area between apertures where the sexine is thickest. The nexine swells at the apertural margins. Each aperture is at the center of a small, deeply sunken pentagonal or hexagonal area, bordered by a broad radially grooved ridge, the slightly irregular radial grooves also extending across the polygonal area but less prominent there than on the marginal ridges. Figs. 4, 5.

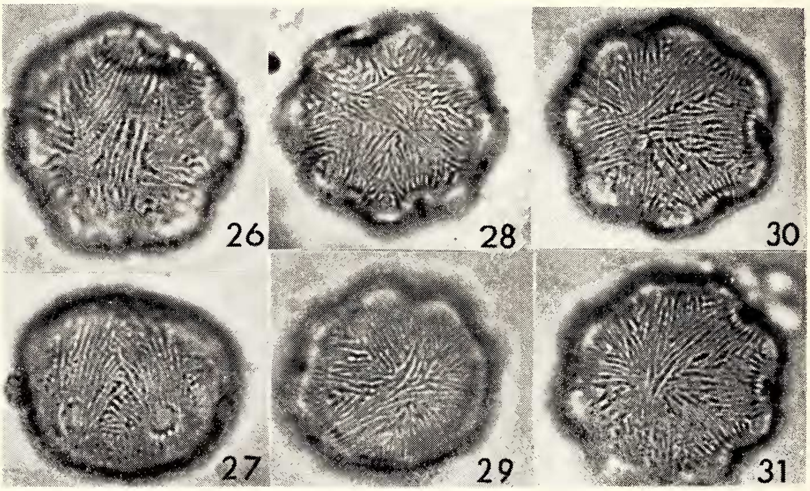
Key to Species of Collomia Based on Pollen Morphology

Pantoporate.
- Apertures at center of sunken pentagonal or hexagonal areas. .... *C. tracyi, C. tinctoria*
- Apertural margin flush, not sunken; sexine with surface of narrow vermiform ridges .... *C. heterophylla*

Stephanoporate.
- Sexine with subparallel ridges whose orientation resembles the pattern of lines of force in a magnetic field having poles at the ends of apertures. .... *C. rawsoniana, C. grandiflora, C. larsenii, C. debilis*
- Sexine with flowing or swirling meandriform ridges.
  - Sexine pattern rather continuous with subparallel ridges in a swirling design. .... *C. diversifolia, C. mazama, C. tenella, C. macrocalyx*
  - Sexine ornamentation of numerous sharply crested, narrow ridges of irregular orientation.
    - Pollen oblate spheroidal .... *C. linearis*
    - Pollen suboblate.
      - Sexine with subradial and irregular ridges locally breaking up into reticulations .... *C. biflora*
      - Sexine with continuous, meandriform ridges .... *C. cavanillesii*

Relation of Pollen Morphology to Taxonomy

In stephanoporate pollen grains the polar diameter is always less than the equatorial diameter. The range of the ratios of equatorial to polar diameters is 1.13:1 to 1.30:1. On the basis of these ratios Erdtman (1952) would consider the stephanoporate grains all to be subspheroidal. Within this category all but *C. linearis* are suboblate; *C. linearis* is oblate spheroidal. The three species with pantoporate pollen grains are, of course, sperical.



Figs. 26–31. Pollen grains of *C. debilis*; 26, polar view showing sexine ornamentation of ssp. *ipomoea*, × 640; 27, view of area slightly above apertures of ssp. *ipomoea*, × 640; 28, 29, polar views of sexine ornamentation of ssp. *trifida*, both × 640; 30, 31, polar views of sexine ornamentation of ssp. *debilis*, both × 640.

The apertures of pantoporate grains are circular and simple, whereas the apertures of stephanoporate grains are composite and ovate. The stephanoporate apertures are intermediate between pori (circular apertures) and colpi (apertures at least twice as long as they are wide) (Erdtman, 1952). In the nexine the apertures are ovate, but the sexine projects over each side of the ovate opening, narrowing it longitudinally to an elongated subrectangular opening in external view. The sexine in most species is composed of small pegs with the tops fused to form ridges. These ridges are seen as the sexine pattern in the external view (figs. 13, 27). The nexine in all the species swells to some extent at the margins of the apertures. This swelling produces light circles around the apertures (figs. 2, 3, 4, 5, 13, 20, 27).

There is some degree of correlation between flower length and grain size (small-flowered plants tend to have small pollen grains), but there is less correlation between grain size and plant size.

A comparison of the species groups based on pollen grain characteristics as found in the above key and the accepted sections of this genus based on other features should show the relation of pollen morphology to taxonomy. The following sections and their species are currently accepted (Wherry, 1944; Grant, 1959):

Collomiastrum Brand: *C. mazama*; *C. rawsoniana*; *C. larsenii*; *C. debilis.*

Courtoisia (Reichenb.) Wherry: *C. heterophylla*; *C. diversifolia.*

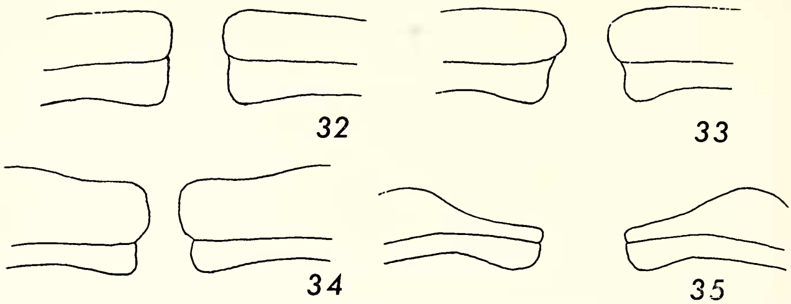
Collomia: *C. cavanillesii*; *C. grandiflora*; *C. linearis*; *C. macrocalyx*; *C. tinctoria*; *C. tenella*; *C. tracyi*; *C. biflora.*

Some discrepancies are immediately evident in a comparison of these sections and the key to species based on pollen morphology. The pollen grain morphology seems to indicate that the section *Collomiastrum* stands well as a unit except for the inclusion of *C. mazama,* whose grains are somewhat smaller and whose sexine pattern is not as striate as *C. grandiflora.* Although *C. grandiflora* has slightly larger grains, it seems to fit better into this section because its sexine ornamentation is almost identical to that of the other species of *Collomiastrum.*

The section *Courtoisia* is not at all homogeneous according to pollen morphology. *Collomia diversifolia* was formerly not recognized as differing from *C. heterophylla,* but the pollen grains of *C. heterophylla* are pantoporate whereas those of *C. diversifolia* are stephanoporate, and furthermore, the sexine patterns are different, strongly supporting their separation into two species. The sexine ornamentation of *C. heterophylla* closely resembles that of *C. linearis,* but spherical shape, pantoporate apertures and sexine pattern of *C. heterophylla* differ from other *Collomia* species, even including *C. diversifolia.* Thus, Wherry's statement (1944) that *C. diversifolia* deserves perhaps only subspecies status under *C. heterophylla* is not supported by pollen morphology.

Three species of the *Collomia* section, i.e., *C. cavanillesii, C. biflora,* and *C. linearis,* have very similar pollen morphology, but the other species assigned to this section are dissimilar in differing degrees. *C. tenella* and *C. macrocalyx* do not have the sharply curved ridges in the sexine of *C. cavanillesii, C. biflora,* and *C. linearis. C. tenella* and *C. macrocalyx* have a sexine pattern similar to *C. diversifolia* and *C. mazama. C. tenella* has a smaller ratio of equatorial to polar diameter and a smaller grain size than does *C. macrocalyx*; furthermore, the number of apertures is usually smaller. Some grains of *C. tenella* have six apertures, but never nine, while *C. macrocalyx* never has six apertures, but sometimes has nine.

The remaining species of the *Collomia* section, *C. tinctoria* and *C. tracyi,* present an interesting problem. The pollen grains of these two species do not resemble any other pollen types in this genus, except that they have a pantoporate arrangement of simple apertures in common with *C. heterophylla.* However, the sexine pattern of *C. heterophylla* shows no resemblance to those of *C. tinctoria* and *C. tracyi.* The peculiar pollen



Figs. 32–35. Diagrammatic optical sections of apertural regions; 32, *C. heterophylla*; 33, *C. linearis*; 34, *C. rawsoniana*; 35, *C. tinctoria*. The upper layer is the sexine; the lower, the nexine.

morphology of the latter two species leaves doubtful their inclusion in this genus.

It is perhaps more than coincidence that *C. linearis,* one of the two North American species with the most southerly range, more closely resembles the two South American species (*C. biflora* and *C. cavanillesii*) in pollen sexine pattern than does any of the other North American species. Pollen of *C. grandiflora,* the second southward ranging North American species, most closely approximates that of the two South American species in size and shape, and has a ratio of equatorial to polar diameter almost identical to that of *C. biflora,* but this species differs in sexine pattern. Thus the geographically closer species also show greater agreement with respect to their pollen grain morphology.

Possibly the similarities and dissimilarities in pollen morphology of the various species might suggest a restudy or reevaluation of additional characters as a step in determining more closely the natural relationships.

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